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Food quality and Hydropsychid caddisfly density in a lake-outlet stream in Glacier National Park Montana

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Food Quality and Hydropsychid Caddisfly Density in a Lake-Outlet Stream in Glacier National Park, Montana

by

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Food Quality and Hydropsychid Caddisfly Density in a Lake Outlet Stream in Glacier National Park, Montana, USA (55 pp.)

Director: J.A. Stanford

Population densities of Hydropsychid caddisflies averaged 6500/m^2 in the lake outlet, but numbers decreased to 1427/m^2 and 209/m^2 at a distance of 200 and 3400 meters downstream. Log transformed total number of hydropsychids regressed strongly on log transformed distance downstream (r^2=.60, p<.01). We examined quantity (POC) and quality (ATP,protein) of seston as a forage base in an attempt to explain the packing of hydropsychids in the lake outlet. Seston concentrations, determined monthly, did not differ significantly between sites except in May and June of 1984 when POC values were signifcantly higher downstream at site III. Only in September of 1984 was significantly more POC found in the lake outlet. ATP concentrations were significantly higher in the lake outlet during the summer months of high lake productivity and during January of 1985. Monthly values of particulate protein regressed strongly on log transformed distance downstream. Stable substrate, discharge and temperature regimes combined with a plentiful supply of high quality food maintain high densities of filter-feeding hydropsychids in the lake outlet. Downstream populations are limited by the introduction of greater abiotic variation (i.e. discharge, substrate, diel temperature) and by a concomitant decrease in seston food quality.

ACKNOWLEDGMENTS

I would like to thank Dr. Jack Stanford for his time, guidance and advice. Without fail he weathered the many storms associated with this effort (Suburban et al.) and I truly appreciate all that he has taught me(despite his being a Celtic fan).

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My family, Bryan Sr., Rachel, Bryan Jr., Matthew and Melee Kaye, all deserve credit as they helped me in the field, at home, and at the cabin.

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As an overall educational experience I highly recommend the staff, facilities and attitudes at UMBS. It is easy these days to pursue goals (professions, images) more directed toward success in a financial context, but the pursuit of knowledge and understanding of ecosystems entails its own rewards. Unfortunately,it appears that only after man has ignored environmental priorities ever so excessivly may we natural scientists play an unwanted, but essential, role in re-educating peoples and re-establishing natural security.

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FOOD QUALITY and HYDROPSYCHID CADDISFLY DENSITY in a LAKE OUTLET STREAM in GLACIER NATIONAL PARK, MONTANA, USA

by H.M. Valett

INTRODUCTION

Food quality has been defined as the "growth producing nutritive content per unit mass" (Cummins 1974, Ward and Cummins 1979). Research has shown that variations in the food quality of their diets can effect the growth of terrestrial insects (Lewis 1984), litter-dwelling arthropods (Bultman and Vetz 1984), gastropod molluscs (Thomas et al. 1983) and aquatic insects (Cummins 1974.)

Organic drift, seston, is an important energy source for many communities in lotic ecosystems (Hynes1970a) and is generally thought to comprise the main forage base of many filter-feeding insects in streams(Wallace et al. 1977, M^{C}Cullough et al. 1979, Wallace and Merritt 1980). Work has been done under laboratory conditions to assess the relative quality of various sources of food for particular

filter-feeding aquatic insects (Anderson and Cummins 1979, Ward and Cummins 1979, Fuller and Mackay 1980, Shepard and Minshall 1981, Hanson et al. 1983, Richardson 1984), whereas few studies have considered the food quality of seston as it is encountered by suspension feeders in situ (Sedell et al. 1978, Naiman and Sedell 1979, Naiman 1984).

The distribution and life history dynamics of filter-feeding populations of aquatic insects, which often dominate zoobenthic biomass, are directly related to the quantity and size of suspended material available for filtering (Carlsson et al. 1977, Colbo and Porter 1979, Fuller and Mackay 1981). By altering rates of development foodquality may play a more vital role in the life cycles of aquatic insects (Cummins 1973, Anderson and Cummins 1979, Ward and Cummins 1979, Hauer and Stanford 1982a), particularly in regard to net-spinning caddisflies (Benke and Wallace 1980, Georgian and Wallace 1981). However, a clear relationship between seston quantity and quality, as a determinant of the density and distribution of filter-feeding stream insects, has not been demonstrated.

Food Quality as an Ecological Factor in Streams

Food quantity, or availability, can be defined as the amount of food per unit environment (Anderson and Cummins 1979). Hynes (1970a) stated that "the availability of food is an obvious factor controlling the occurrence and

abundance of benthic invertebrate species." Stream ecologists have emphasized food quality as an important, if not determinant, factor affecting the growth rate and survivorship of aquatic insects (Carlsson et al. 1977, Mackay 1979, Ward and Cummins 1979).

Particulate and dissolved organic carbon represent an important energy resource in aquatic systems (Cummins 1974, Wallace et al. 1977, Wallace and Merritt 1980). Work on the distribution of filter feeders has utilized the analysis of organic carbon to characterize the food availbality in particular stream reaches (Erman and Chouteau 1979, Hauer and Stanford 1982b). However, not all organic carbon in stream seston is biochemically available to aquatic insects. This refractory (unuseable) material is considered a low quality food source. In contrast, other organic material is highly labile and is easily assimilated. Cummins (1974) suggested that the microbial flora colonizing particulate organic matter in streams is highly labile, while the organic substrate itself may be highly refractory and unuseable by insects. Other work on the trophic relations of aquatic insects has shown that variations in the protein content of insect diets have caused significant changes in larval growth patterns (Cummins 1973). Total protein has been used as a measure of labile organic matter and, therefore, as an indication of food quality in situ.

(Statzner 1978, Kondratieff and Simmons 1984).

Particulate organic matter is composed of nonviable substrates (e.g. riparian-derived leaves, algal filaments) and microbial biomass, which causes decomposition of the organic substrates. Cummins (1974) proposed that macroinvertebrate detritivores were nutritonally dependent on the microbial flora of the particulate matter, rather than on the organic substrate itself. Karl (1980) stated that, despite some problems, adenosin triphosphate (ATP) assays are probably the only convenient and reliable method for assessing microbial biomass in most environmental samples. Wallace et al. (1982) used ATP to measure food quality in a southern Appalachian stream. Ward and Cummins (1979) utilized ATP assay, along with other parameters, when they assessed the effect of variability in food quality on the growth of a stream detritivore. Results of their study indicated that larval growth was most strongly correlated with ATP content as opposed to substrate respiration rates or total carbon and nitrogen.

Gut analysis has been used by many researchers to relate filter feeders to components of seston as a resource base (Cummins 1973, Malas and Wallace 1977, Wotton 1978, Fuller and Mackay 1981, Hauer and Stanford 1981, Ross and Wallace 1981). Recently, work on hydropsychid caddis larvae in a lake outlet has utilized gut analysis to describe the

phenology and food of those filter-feeding larvae (Xiang et al. 1984). Typically gut analysis has included quantitation of the contents of the stomodaeum of larvae collected in situ. This method of analysis allows one to characterize larval feeding habits based upon food that has already been ingested. Examining the gut contents of the filter-feeding larvae may characterize what has been ingested, but does not directly describe the quality of the available seston.

Temporal and spatial features of stream mechanics and chemistry (e.g. substrate stability, discharge, stream conductivity and alkalinity) may also influence the distribution of filter-feeding caddisflies. Concentrations of dissolved solids is of particular interest as hard-water streams have been shown to be more productive than streams with relatively low alkalinity (Hill and Webster 1982). Krueger and Waters (1983) have noted that the secondary productivity of benthic invertebrates may be directly linked to the total alkalinity of the stream water. They suggest that alkalinity may affect invertebrate populations by altering detrital decomposition rates and by altering the rate of flocculation and precipitation of dissolved organic carbon.

The Lake Outlet System

Dense populations of filter-feeding aquatic insects have been noted in lake outlets (Ulfstrand 1968, Carlsson et al. 1977, Sheldon and Oswood 1977, Wotton 1978, Oswood 1979). This phenomenon is apparently associated with the discharge of high quantity and quality seston from the epilimnion of the lake. Sheldon and Oswood(1977) formulated a predictive model implicating decreasing seston concentrations as the explanation for decreasing numbers of filter-feeding blackfly larvae downstream from a lake outlet. Field measurements indicated, however, that seston concentrations increased slightly downstream from the lake outlet while numbers of blackflies decreased. In a similar study Oswood (1979) quantified the densities of filter-feeding Hydropsychid caddsifly larvae along the same outlet system. He noted a precipitous downstream decline in larval abundance, accompanied by an unexpected increase in seston concentrations. Brönmark and Malmqvist (1984) observed the characteristic decrease in numbers of filter feeders below a Swedish lake, but were unable to show a concomitant decrease in seston concentration. It is unlikely, therefore, that a decrease in the availability of seston causes the noted decrease in the density of filter-feeding insects downstream in lake outlet systems.

Some work has suggested that efficient filtering and

processing near the lake's outlet alters the quality of the stream seston (Ulfstrand 1968, Carlsson et al. 1977, Oswood 1979, Benke and Wallace 1980). Benke and Wallace (1980) found that some net-spinning caddisflies in an Appalachian stream were net producers of detritus. A visual determination of seston composition revealed that detritus, as opposed to cellualr components, increased from 10% of its maximum, near the lake outlet, to nearly 100% one kilometer downstream in a Montana mesotrophic lake outlet (Sheldon and Oswood 1977). Similarly, Maciolek and Tunzi (1968) noted a progressive decrease in cellular microseston downstream from a lake outlet, while noting a relative increase in detritus. Carlsson et al. (1977) suggested that it was the nutritive value of seston particles which was confining the huge population of blackfly larvae to the outlet of a lake in Sweden. Oswood (1979) suggested that high densities of net-spinning caddisflies in a Montana lake outlet were limited by the quality of available seston. None of these studies clearly investigate the role of food quality versus food quantity in delimiting the distribution of particle feeding insects in lake outlets.

Therefore, this study was undertaken to differentiate quantity (i.e. concentration of particulate organic carbon) versus quality (i.e. protein and ATP concentrations) in seston (i.e. transported organic material) in relation to

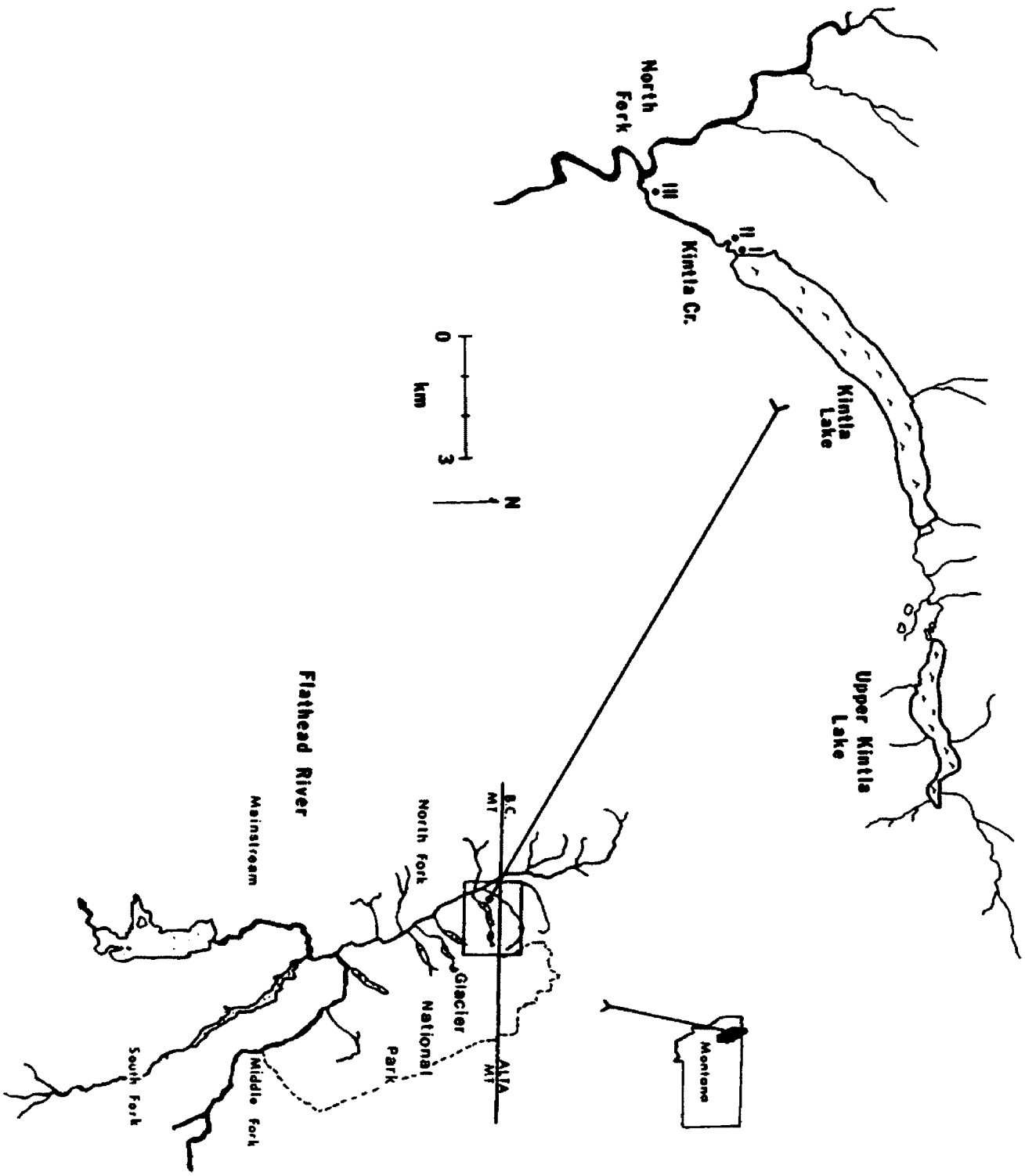
the density and distribution of filter-feeding Hydropsychid caddisflies in a lake outlet stream. Food quality and quantity variables were measured in time series, along with important habitat variables (e.g. temperature and substrate dynamics) and correlated with measured density of the hydropsychid community in three sequential reaches downstream from the lake outlet.

METHODS AND MATERIALS

Study Site and Sampling Design

The Flathead River originates in the mountains of the Continental Divide in northwest Montana and southwest British Columbia. Headwater streams proceeding from cold springs or snow melt feed the three main forks of the Flathead. Lower order streams are canopied by Douglas fir and western larch. The North Fork of the Flathead is fed by many small streams originating from lake systems along the western slope of Glacier National Park. Just south of the US-Canada border, the Kintla Lake system is the first lake-stream system to feed the waters of the North Fork (Fig. 1). Two lakes are located in the Kintla drainage. Water from Upper Kintla Lake drains into the larger Kintla Lake, which has a maximum depth of 122.6 meters. Kintla Creek originates from the southwestern end of Kintla Lake at

Figure 1. The Kintla Creek drainage in northwestern Montana, USA, and the study sites in the outlet of Kintla Lake.



1222 meters elevation and drops 91 meters as it flows through glacial till to the tertiary sediments of the North Fork valley 4.5 kilometers downstream. Hauer et al. (1980) studied the distribution of aquatic insects in the Kintla drainage and noted that caddisflies of the genus Hydropsyche were present only below Kintla Lake and that they were present in great numbers in the lake's outlet. Other research on lake outlets in northwestern Montana included similar observations on the caddisflies of the Kintla Lake outlet (Appert 1977).

Three sample sites were established on Kintla Creek. Station I was located 10 meters downstream from the lake outlet. Site II was approximately 200 meters downstream from the outlet, and site III was established 3.5 kilometers downstream from the lake outlet just before Kintla Creek flows into the North Fork of the Flathead River.

Particulate organic carbon (POC) concentration in seston was measured at each site throughout the duration of the study period. One 500 ml sample was collected in a polyurythane bottle and was either processed within 24 hrs or was preserved with one ml of concentrated H_2SO_4. Duplicate samples were taken at site I in August 1984 and at site III in January of 1985. POC values were determined by CO_2 liberation procedure (Menzel and Vaccaro 1964) on an Oceanography International 0524B total carbon

system.

Protein samples were collected in triplicate from each of the sample locations. Each sample contained the filtered contents of four liters of water taken from midstream. Care was taken to keep benthic matter out of the grab sample while pushing the collecting bottle through the water column. The Brilliant Blue G-250 protein analysis procedure (Bradford 1976) and the Bio-Rad Protein Assay Kit (Bio-Rad Laboratories) were used to quantify soluable protein in the seston samples. I utilized this assay with some modifications described by Beardon (1979) and Setchell (1981). See appendix A for further details.

Triplicate ATP samples were collected monthly in one liter polypropylene bottles from each station. Samples were analyzed for ATP immediatly upon returning to the laboratory. Using the Lab-Line ATP photometer we followed the newly described technique presented in the Turner Luminescence Review(1983). This method utilizes a cold extraction of ATP from filtered seston and the quantitation of emitted light when the extracted medium is combined with luciferin-luciferase enzyme in the ATP photometer.

Benthic invertebrates along the Kintla outlet system were sampled using a modified kicknet procedure following Hauer and Stanford (1981) in which the kicknet is held firmly against the substrate as large rocks above the net

are cleaned off while being held in the stream near the mouth of the net. After 45 seconds of cleaning rocks in this manner the benthos of the .36 m^2 area immediatly upstream of the net is agitated by hand and foot action for 15 seconds. All liberated material was collected in the net and preserved with 10% formaldehyde. Samples which were to be used for gut analysis were first inundated with bicarbonate in order to asphyxiate larvae. Hydropsychid larvae were then picked from the benthic samples, identified and counted in order to establish population densities.

Cummins (1973) described a method for examination of insect gut contents which considers the relative amounts of animal matter, algae and detritus present in the foregut. This method entails the dispersion of foregut contents onto a filter for observation under the light microscope. Fuller and Mackay (1981) described a slight modification of the technique used by Cummins. The modification entails the "sonification" of the ingested foregut material to ensure the separation of compressed gut contents. In this study the foregut contents of three hydropsychid larvae were combined on one cleared filter. Representative drawings of eight fields from each slide were made and gut materials were classified as: 1) animal matter, 2) plant matter, and 3) detritus. Foregut composition is reported as percent area of food type.

Temperature data for the different sites were recorded as often as possible using continuous thermographs at stations I and III. Total alkalinity, conductivity and discharge was measured monthly.

Collecting and analysis began in March of 1984 and continued through March of 1985. Samples of benthic invertebrates were taken in October and December of 1983. Seston and water samples were collected monthly for the duration of the study. Samples were analyzed for all food quality parameters. Foregut analysis was carried out on caddisfly larvae collected during November and December of 1983.

RESULTS AND DISCUSSION

Hydropsychid Distribution

Total number of Hydropsychidae decreased dramatically with distance downstream from the outlet (Fig. 2, Table 1). The geometric mean for site I was 1499 larvae/m^2, whereas 200 meters downstream at site II the geomertic mean

Figure 2. Abundance of larval hydropsychids regressed against distance downstream from the Kintla Lake outlet. Data are log transformed and solid circles are geometric means for each sample site.

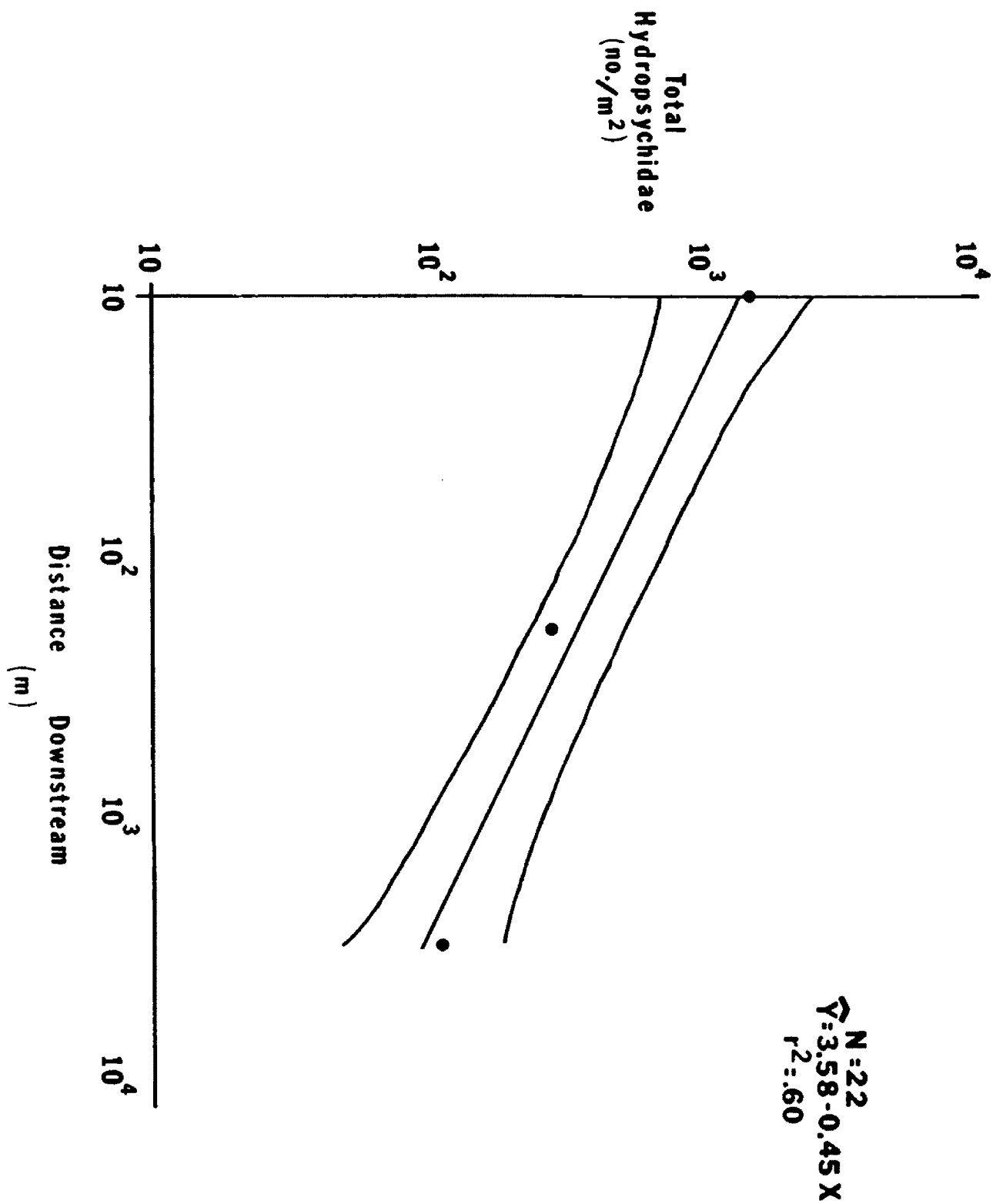


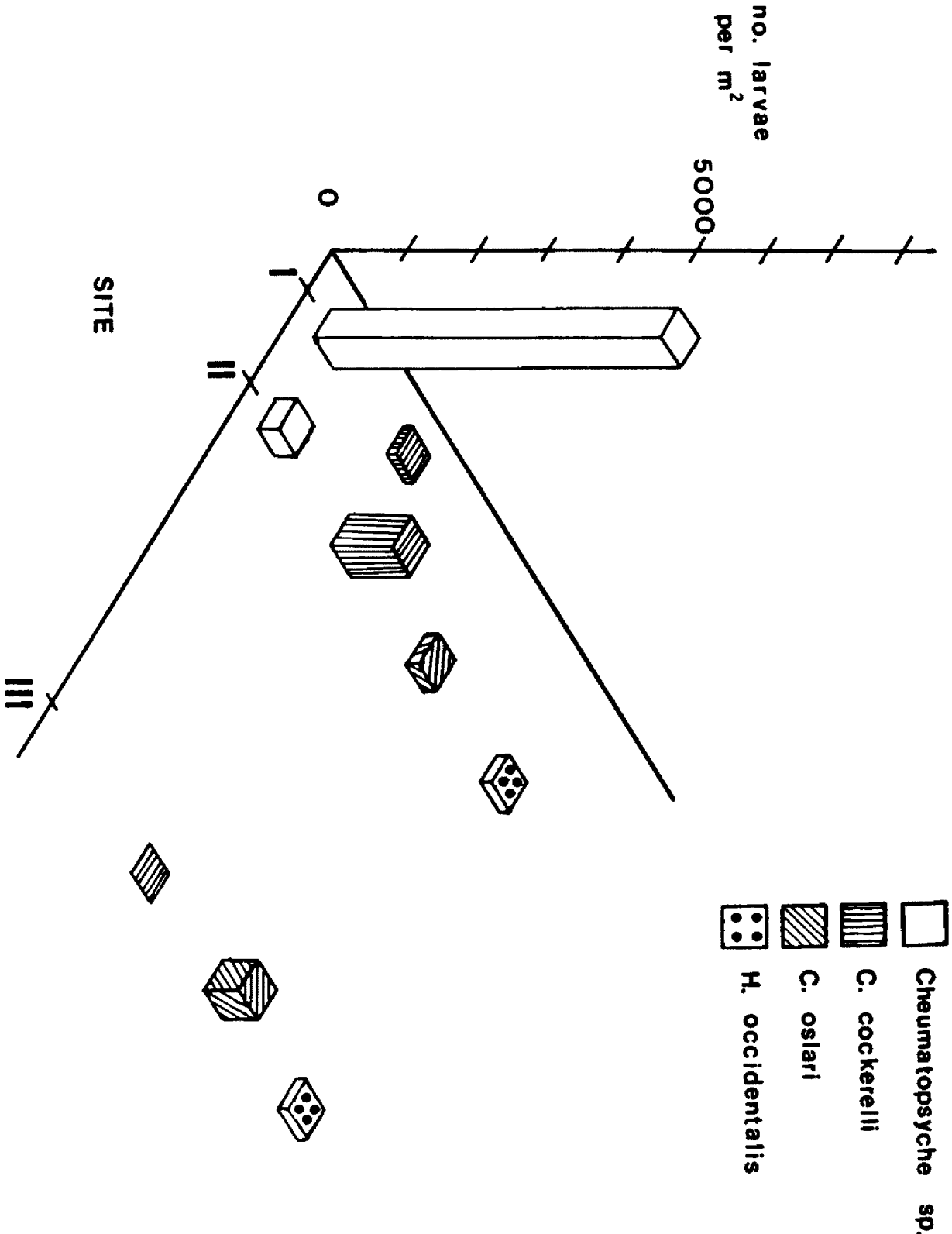
Table 1. ANOVA table for linear regression shown in Fig. 2. Dependent variable (larval abundance) and independent variable (distance downstream) are log transformed. Significance of regression MS tested against residual MS.

Source of Variation	SS	Df	MS	F	
Total	7.466	21			
Regression	4.464	1	4.464	29.76	$P < .001$
Residual	3.002	20	0.150		
Lack of linear fit	0.098	1	0.098	0.64	n.s.
Pure error	2.904	19	0.153		

dropped to 287 larvae/m^2. The geometric mean for site III was 113 larvae/m^2. Statzner (1978) noted a drastic decrease in larval densities within a similar distance downstream from a lake in West Germany.

Species composition within the Hydropsychidae also changed as distance from the outlet increased. Cheumatopsyche sp. were clearly the dominant larvae in the Kintla Lake outlet comprising 99% of the individuals collected at site I (Fig 3). Ceratopsyche cockerelli larvae were found only sparsely in the outlet and were the only other Hydropsychid collected at that site. At site II C. cockerelli comprised 56% of the comparatively few larvae that were present, while Cheumatopsyche sp. accounted for 25% of the total. Ceratopsyche oslari and Hydropsyche occidentalis comprised only 10% and 9% of the larvae collected at site II. No Cheumatopsyche sp. and only a few C. cockerelli (< 15 larvae) were collected from site III. C. oslari and H. occidentalis were the dominant species at site III. Similar sequential changes in hydropsychid fauna has been observed elswhere in the Flathead River system (Hauer and Stanford 1983) and for other systems (Hildrew and Edington 1979). These studies placed temperture and food abundance as primary controls on the distribution of individual species within a stream continuum.

Figure 3. Distribution of Hydropsychidae larvae downstream from the Kintla Lake outlet in December 1983.



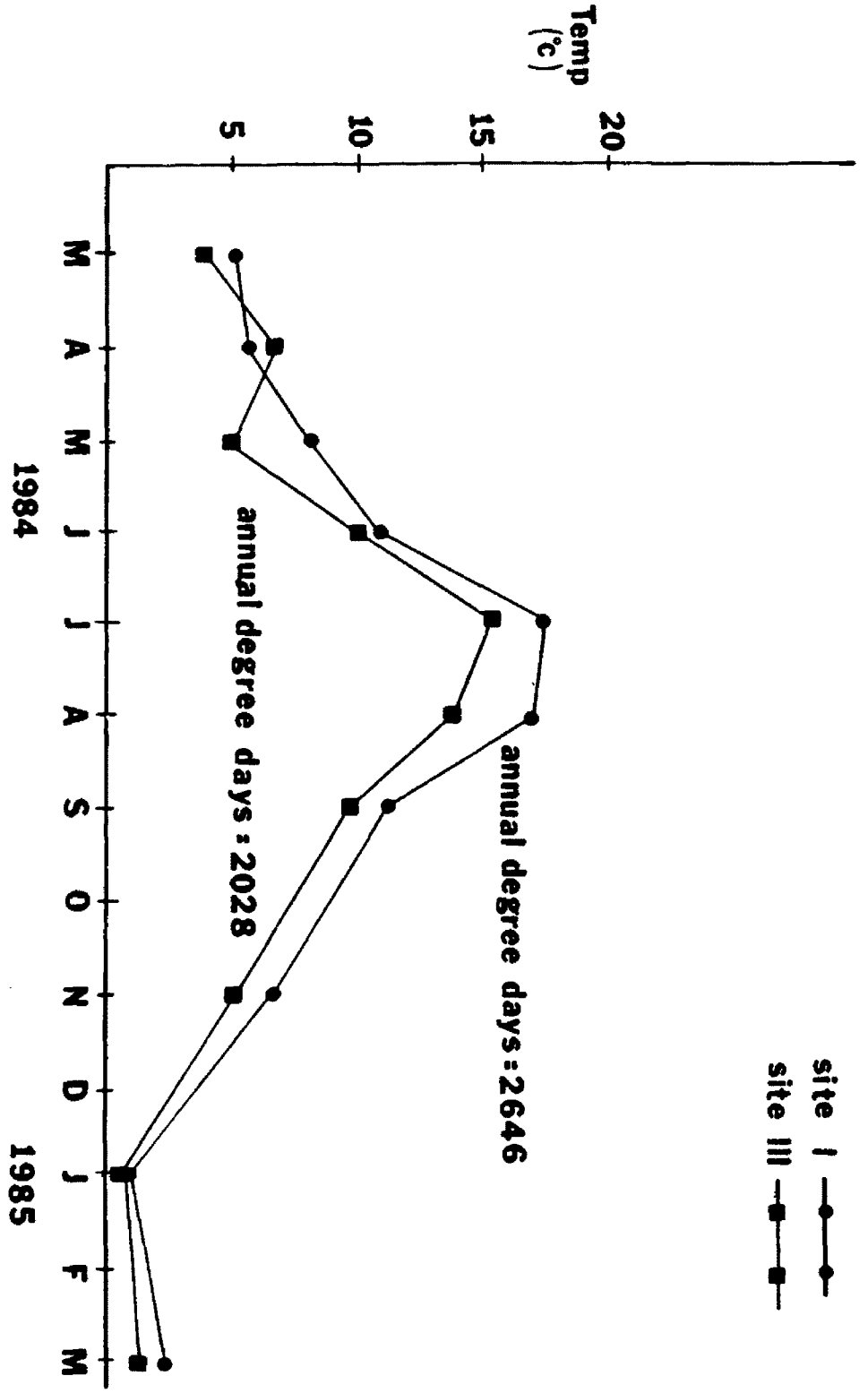
Physical Variables

Discharge from Kintla Lake reached a minimum of Ø.27 m^3/s in March of 1985. Maximum discharge during the study period was 14.21 m^3/s in June of 1984. Average total alkalinity was 6Ø mg $CaCO_3/l$ and varied only two milligrams per liter between sites. Conductivity values were similar, averaging 1Ø2, 1Ø4. and 1Ø9 umhos/cm at sites I, II and III respectively. See appendix B.4 for actual data.

Kintla Lake was ice-covered from Jaunary to March 1985. No ice was observed on the outlet, while ice frequently spanned the channel downstream at site III. Water temperature at the outlet was consistently higher than at site III (Fig. 4). Annual degree days accumulated at site III was only 2Ø28 as compared to 2646 in the lake outlet.

Substrate disturbance (e.g. displaced rocks) was rarely observed in the outlet. The substrate was typically anchored by heavy growths of the filamentous green alga Zygnema and by mats of the stalked diatom Gomphonema. The algal mat was significantly reduced at site two, but included large amounts of benthic moss. Oswood (1979) found significantly greater mumbers of hydropsychid larvae associated with moss in Owl Creek, another Montana lake outlet system. This suggests that hydropsychid population densities at site II may be exaggerated and that even sparser populations may exist in areas not supplemented with benthic mosses.

Figure 4. Comparison of the annual temperature profile and accumulated degree days in the Kintla Lake outlet (site I) and 3.4 km downstream (site III).



Algal growth was limited to a thin epilithic, diatom film at site III and the substrate was comprised of loose fine-grained material along with less firmly anchored rocks.

The presence of moss may also have been indicative of CO_2-rich groundwater intrusion below the outlet proper (Hynes 1970a). Site III averaged 40% greater discharge than was measured at site I (see Appendix B.4), which further suggests ground water influences, since no tributaries enter Kintla Creek between the lake and the North Fork of the Flathead River.

Food Quality and Quantity

Particulate organic carbon values were generally the same at all sites, except during May and June of 1984 when significantlygreater amounts of POC were found at site III (Table 2). Only in September 1984 were POC concentrations significantly higher in the outlet and at site II than downstream at site III. In January of 1985 POC values were significantly higher in the outlet as compared to concentrations at site III during the same month.

Total protein concentrations were consistently higher at the upstream sites (Fig. 5). Regression of total protein against distance downstream from lake outfall showed that protein concentrations decreased linearly after log transformation of the distance downstream during all but two months of the study (Table 3). This differs markedly with

Table 2. Relationship between POC content (mgC/l) of the seston and distance from the lake outlet. Boxed data (means) were not significantly different (P <.05) per the Newman - Keul's multiple range test.

Site		Date								
		Mar	Apr	May	Jun	Jul	Aug	Sep	Nov	Jan
I	X	0.081	0.160	0.167	0.164	0.114	0.245	0.308	0.067	0.132
(.01 km)	95% CI	0.035	0.064	0.055	0.126	0.042	0.022	0.025	0.047	0.094
II	X	0.056	0.186	0.173	0.214	0.150	0.270	0.285	0.246	0.143
(.20 km)	95% CI	0.042	0.034	0.087	0.006	0.045	0.030	0.049	0.295	0.027
III	X	0.017	0.193	0.248	0.222	0.141	0.248	0.258	0.104	0.061
(3.4 km)	95% CI	0.063	0.584	0.052	0.004	0.059	0.022	0.022	0.099	0.025

Figure 5. Relationship between monthly concentration (mean) of particulate protein in seston and distance downstream from the lake outlet.

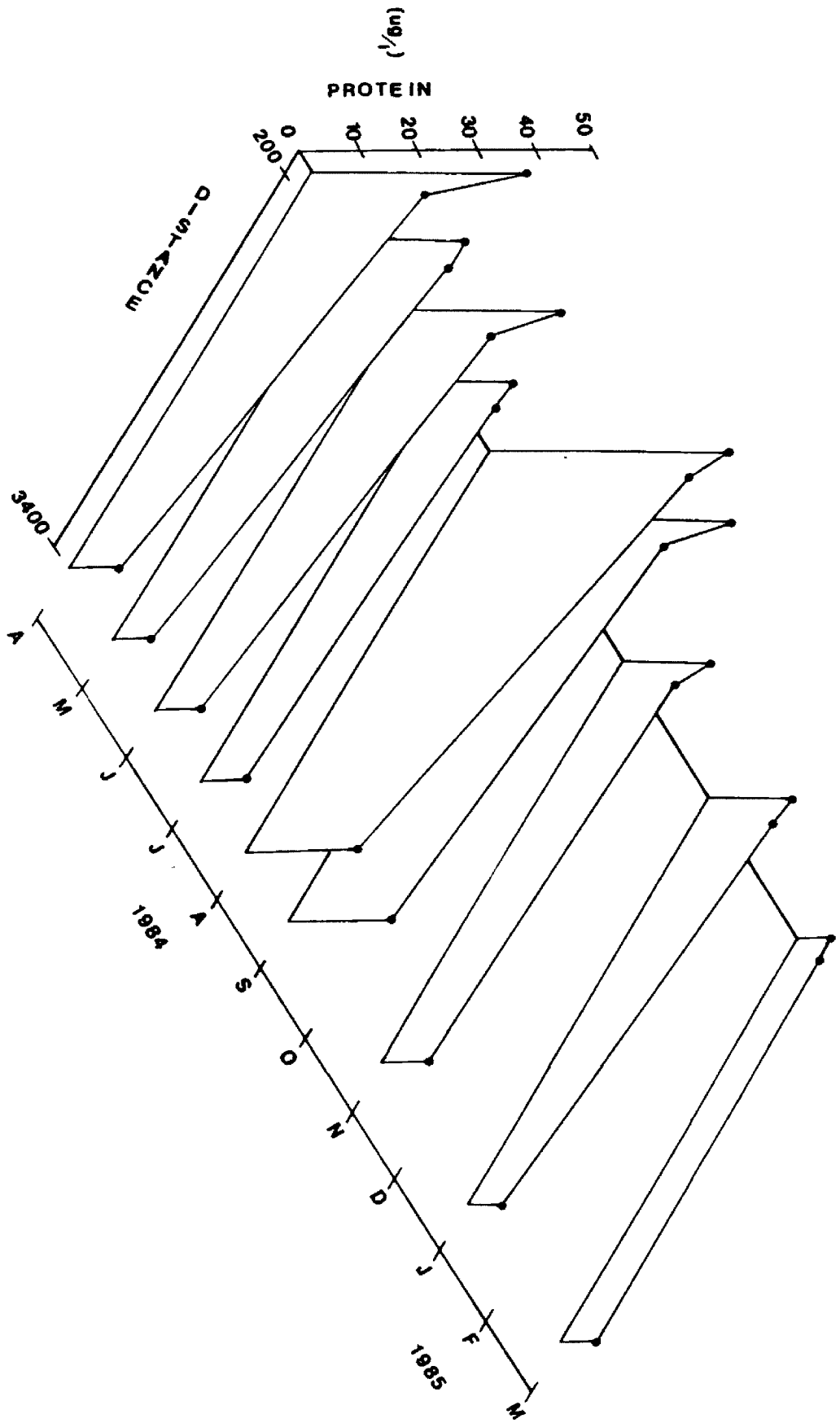


Table 3. Regression equations and coefficients of determination (r^2) for linear regression of log transformed independent variable (distance downstream) and dependent variable (protein concentration).
* = P <.05, ** = P < .01, *** = P < .001, ns = not significant

Month	Regression Equation	r^2	
April '84	Y = 44.08 - 9.90X	.92	***
May	Y = 26.28 - 4.98X	.61	*
June	Y = 35.40 - 7.90X	.77	**
July	Y = 12.50 - 1.21X	.19	ns
August	Y = 52.80 - 8.52X	.61	*
September	Y = 40.90 - 6.51X	.87	**
November	Y = 16.80 - 2.15X	.94	**
January '85	Y = 19.10 - 3.4X	.66	*

Statzner (1978), who found no significant changes in the protein concentrations downstream from a West German lake outlet.

ATP values varied significantly during June, Julyand September, when concentrations at site I were significantly higher than at sites II or III, and during January 1985 when significantly less ATP was present downstream at site III (Table 4).

Analysis of 30 larval foreguts indicated that percent animal matter remained relatively constant betweensites, while detritus content increased from 46% at site I to 63% at site II and a maximum of 86% at site III. Relative amount of plant matter decreased with distance downstream comprising 47, 28, and 12 percent of gut content at sites I, II and III respectively.

I concluded that while the total concentration of seston (food quantity) was about equal between sites downstream from the lake, a measurable decrease in the labile food items (food quality) was apparent at least between the upstream sites and site III. Protein and ATP data suggested that the biotic component of the seston (zoo- and phytoplankton) decreased significantly within 200 meters downstream from the outlet.

Table 4. Relationship between ATP content (ng/l) of the seston and distance downstream from the lake outlet. Boxed data (means) were not significantly different (P <.10) per the Newman - Keul's multiple range test.

Site		Date								
		Mar	Apr	May	Jun	Jul	Sep	Nov	Jan	Mar
I	X	0.554	3.920	1.220	4.560	2.060	2.950	2.020	2.510	1.060
(.01 km)	95% CI	0.245	6.100	2.350	7.714	6.100	2.191	3.790	2.022	0.298
II	X	0.617	1.090	3.070	1.590	0.830	1.300	2.340	2.920	1.890
(.20 km)	95% CI	0.362	1.560	7.580	1.040	0.893	1.360	1.390	0.446	1.960
III	X	0.442	1.820	1.140	0.880	1.030	1.430	2.030	0.932	1.280
(3.4 km)	95% CI	0.302	2.700	0.573	0.174	2.130	3.500	0.431	2.330	0.471

Ecological Ramifications

Recent work on lake outlets has evoked the causality of food quality and quantity (Bronmark and Malmqvist 1984, Kondratieff and Simmons 1984, Richardson 1984) and species interaction (Statzner 1978) in explaining the density and distribution of the filter-feeding zoobenthos of lake outlet systems. Additionally, Müller (1982) demonstrated that adult caddisflies below a lake outlet will fly in an upstream direction and oviposit on the lake surface. He suggested that the withdrawl current eventually returns the nymphs to the outlet, thus maintaining high population densities. These hypotheses are not necessarily mutually exclusive. Inherent in this colonization cycle concept is the existence in the outlet of a substantial amount of high quality food for the accumulation of biomass and the successful completion of metamorphosis. Data presented herein show that such a resource base exists for caddisflies located in the Kintla Lake outlet.

Some authors have stressed the need to investigate food quality and temperature interactions (Cummins 1973, Anderson and Cummins 1979, Ward and Cummins 1979, Fuller and Mackay 1980, Hanson et al. 1983) because the rate of microbial production and decomposition, and hence the supply of high quality food, may be temperature dependent. As a measure of

food quality Naiman(1984) reported different respiration rates associated with size classes of seston collected from streams of different orders. He did not, however, address the effects of the different thermal regimes from which the seston was collected. Anderson and Cummins (1979) stressed that temperature will affect aquatic insects directly by affecting animal metabolic rates and indirectly by establishing food quality and quantity. Ward and Stanford (1982) maintained that the general distribution of all aquatic insects is primarily due to the thermal regimes encountered. Biomass and productivity may be related to food quantity or quality interacting with temperature constraints on metabolism. The downstream reaches of river systems are generally warmer than upstream portions (Hynes 1970a) and, due greater heat capacity larger channels manifest a more constant thermal environment (Vannotte et al. 1980). Similarly, the large heat capacity of lakes contribute a more stable thermal regime in their outflow streams(Ulfstrand 1968, Hynes 1970a). Indeed, Hynes (1970b) stated that "the observed distribution of some lake outlet aquatic insects is due primarily to the thermal regime". In this study of the Kintla Lake outlet system the sequential replacement of Cheumatopsyche by Ceratopsyche and Hydropsyche may reflect the existence of different thermal regimes within this relatively short stream segment.

Hydropsychid distribution may, therefore, be directly dependent on temperature while population density may be determined by food quality and species interaction as suggested by Cummins(1974), Statzner(1978) and Ward and Stanford (1982).

Similar to lake outlets, the zoobenthos in the tailwaters of some surface-release impoundments is dominated by Hydropsychid caddisflies and other filter-feeding insects,such as Simuliidae (Ward and Stanford 1980). Tailwater temperatures may be elevated in a manner similar to lake outlets discussed above. Ward and Stanford's "Discontinuity Distance" (1983a) measures the longitudinal shift (- : upstream, + : downstream) of a given parameter due to stream regulation. Following their reasoning, a negative temperature discontinuity caused by Kintla Lake may explain the observed shift in species composition in the outlet stream. Indeed, Cheumatopsyche dominate the hydropsychid community in the tailwaters of the epilimneal-release dam on the regulated portion of the Flathead River below Flathead Lake (Stanford: pers. comm.). Similarly, Hauer and Stanford (1983) demonstrated a positive thermal discontinuity associated with dominance by the more stenothermic Arctopsyche grandis. A. grandis is common in all 3rd and 4th order streams in the Flathead, not regulated by lakes. But none were found in the Kintla Lake outlet

stream.

Continuous input of lake-derived seston (allochthonous matter) lends stability to the stream ecosystem (Fisher and Likens 1973). Because large particulates including inorganic sediment are trapped by the lake, outflow streams are not intensely scoured during spates. This lack of severe substrate disturbance allows large mats of benthic algae to grow, which in turn may stabilize the stream bottom(Armitage 1976). Additionally, lakes minimize daily thermal fluctuations creating more predictable diel temperatures. In many ways the outlet may be considered a predictible or constant environment in which biomass can be maximized (Ward and Stanford 1983b).

Although seston was equally plentiful along Kintla Creek, the high densities of hydropsychids found in the Kintla Lake outlet appeared to be supported by the high-quality lake-derived seston. Downstream from the Kintla Lake outlet fluvial processes introduced more abiotic variation and a concomitant reduction in seston food quality effectively limited the larval densities. Groundwater influences and a lesser heat capacity contributed to the colder thermal regime of the downstream reaches of Kintla Creek, whereas, Kintla Lake maintained warmer temperatures in the lake outlet. The distribution of certain hydropsychid caddisflies in Kintla Creek may be determined

by the species' ability to survive in a given thermal regime, while population densities may be determined more by environmental stability and the availability of high-quality food.

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CHAPTER II
APPENDIX A: METHODOLOGY

Appendix A.1 ATP Methodology

Materials

Standards:

Use 1Øug/ml stock solution of Na_2 ATP $3H_2O$ to make 25 ng/ml standard by diluting 25 ul^2 of the stock solution to ten mls with HEPES buffer. A working standard of 25Ø pg/ml can be made from Ø.1 ml of the 25 ng/ml standard by diluting to a total volume of ten mls with HEPES buffer.

Reagents:

- HEPES Buffer, pH 7.5, luminescence purity
- Luciferin-Luciferase, luminescence purity, reconstituted with 5.5 mls HEPES buffer
- Releasing-Reagent, Surfactant B-2 with phosphatase inhibitor

Glassware:

- Scintillation vials, 3/sample
- Filtration apparatus, (column, frit, clamp, catch flask, trap)

- One pair forceps

- 25 mm Gelman Type A/E Glass Fiber Filters, .45 um mesh size
- One vacuum pump apparatus, hand or automated
- One 1000 ml graduated cylinder
- One 0-5 ml autopipet
- One 10-200 ul autopipet
- One Lab-Line ATP Photometer

Procedure:

1. Acid wash all scintillation vials in 10% HCl. Rinse three times with de-ionized water. Place cleaned vials in groups of three/ sample.

2. Rinse graduated cylinder with a small amount of sample and discard. Pour remaining sample into graduated cylinder, record noted volume, and filter using the described filters and filtration apparatus.

3. Carefully remove filter from frit using clean forceps and place in clean,dry scintillation vial. Be careful not to disturb filtered particulate when placing filter in vial.

4. Add 1.0 ml of releasing reagent followed immediatly by 1.0 ml of HEPES buffer. Wait approximatly three minutes.

5. Using 200 ul autopipet transfer 200 ul of the extracted solution to each of the remaining scintillation vials. Remove vial containing remaining extract solution.

6. Set photometer for Integral Mode and 60 second delay with zero=5.0 and sensitivity =7.0.

7. Add 200 ul of HEPES buffer to the first of the two vials containing extracted ATP.

8. Simultaneously activate assay mode on photometer and pipet 200 ul L-L enzyme into vial containing extract and buffer. Cap vial and swirl. Quickly place in photometer.

9. Record value for unknown(R_u). Reset photometer.

10. Autopipet 200 ul of 250 pg/ml standard into the second vial containing 200 ul of extractant.

11. Simultaneously activate assay mode on photometer and pipet 200 ul L-L enzyme into vial containing extract and standard. Cap vial and swirl. Quickly place in photometer.

12. Record value for spike(R_{IS}).

Calcualtions

ATP concentrations are calculated using the following equation as provided by Turner Designs in bulletin no.204.

$$[ATP]=1/V_F \quad R_u/(R_{is}-R_u) \quad [ATP_{std}]$$

where:
[ATP]:concentration of ATP (g/ml)
V_F: volume of water filtered
R_u: counts of unknown
R_{is}: counts of spike
$[ATP_{std}]$: concentration of ATP standard (g/ml)

Appendix A.2 Benthos Processing Procedure

Materials

- two sieves, 150 um mesh
- one large, porcelain tray
- two pair, good quality forceps
- one/taxon, insect vial and cap, label

Procedure

1. Uncap preserved preserved sample and place a manageable amount in a 150um mesh sorting sieve. Thoroughly rinse all preservative from the sample contents.

2. Vigorously rinse all clumps of moss or other vegetation and check for any obvious fauna. Discard the large material including rocks and processed clumps of vegetation.

3. Using a lab marker or grease pencil subdivide a large porcelain tray into six equal areas parallel with the width of the pan.

4. Transfer the contents of the sieve to the porcelain pan and fill with hot tap water until ca. 2" of water is standing in the pan. Discard any large rocks or moss clumps after checking for fauna.

5. Following the lines on the bottom of the pan, steadily

pick all fauna from the water and gravel while proceeding from one end of the tray to the other. Agitate the sample and repeat the procedure in the opposite direction.

6. Place all fauna in appropriate vials marked with the specific taxon, sample date, location, and sample number.

7. Return the picked "refuse" to a second screen of 150um mesh or to a jar for preservation if further processing is to be delayed. This material should be labeled "Macro Refuse" to indicate that the sample has been macro-picked.

8. Continue steps 1-7 until all of the sample has been macro- picked and all macro refuse has been cleaned and collected.

9. Thoroughly rinse macro refuse in a 150um mesh sieve if it has been preserved. Subsample the refuse and remove a manageable amount of the material (usually 1/4) and preserve for further processing. Label the jar as Macro-Refuse-1/4 and include sample number, date and location.

10. Suspend the rinsed subsample of macro-refuse in hot tap water and pick as described in steps 4 & 5 while paying particular attention to the smaller components of the benthos.

11. Placeall specimens into a single vial labeled "Micro-Pick- 1/4". This idicates that the sample has been macro-picked and 1/4 of the macro-refuse has been micro-picked.

12. Returnall micro-refuse to the screen and preserve for further processing. Label the vial "Micro-Refuse 1/4 subsample". Include sample number, date and location.

13. Repeatsteps 1-13 for all samples before continuing the procedure further.

14. Place micro-refuse in the 150um mesh sieve and rinse out preservative.

15. If necessary subsample the micro-refuse until a manageable amount is obtained (usually 1/4) for picking

under the microscope.

16. Using a binocular dissecting microscope carefully sort through the sample picking all benthos and placing the specimens in a single vial marked "Scope-Pick-1/4". This labeling indicates that a 1/4 subsample of the micro-refuse was taken and all fauna was removed while being observed under the microscope.

Calculations

1. All samples were taken from a $\emptyset.36m^2$ area. Densities can be calculated as follows:

(# of ind. in macro-pick) + (# of ind. in micro-pick x micro subsample correction factor (cf)) + (# of ind. in scope-pick x micro cf x scope cf)

2.

Pick Type	Subsample Correction Factor
Macro	none=1
Micro	inverse of subsample fraction of macro refuse picked usually=4
Scope	inverse of the product of subsample fractions from micro picking of macro refuse and scope picking of micro refuse

Appendix A.3 Bio-Rad Protein Assay Procedure

Materials

Standards:

Bovine gamma-globulin standards are used (~ 1500ug/ml). Standards range form 3.75 ug/ml to 280 ug/ml and are obtained by diluting the stock solution with appropriate amounts of ETS buffer.

Reagents:

- ETS Buffer
  1) 0.05% Triton X-100
  2) 75 uM $MgSO_4$
  3) 0.15% Polyvinylpyrolidone
  4) 50 mM Na_3PO_4
- BB-G250 dye

Glassware:

- scintillation vials (1/sample and/or standard)
- filtering apparatus (Thomas mortar and pestel, power drill, ring stand and clamps)
- one pair forceps

- 47mm Gelman Type A/E glass-fiber filters. Ø.45 um mesh
- filtration apparatus (vacuum, column, frit, side arm flask)
- 3 beakers @ 25Ø ml
- 1-5 autopipet
- Ø-2ØØ ul pipet
- two glass cuvettes (not equal to quartz), 1 cm light path
- centrifuge
- squirt bottle with DI rinse water

Procedure:

Reagent preparation

1) Reconstitute bovine gamma-gloulin by adding 2Ø ml of DIHOH.Stored at Ø-4C. Its shelf life is 6Ø days. Frozen at -2ØC it will last for six months.

2) Prepare BB-G25Ø dye by diluting one part of concentrated dye with four parts DI water. Filter the diltued dye through a glass-fiber filter and store at cold temperatures. At room temperature cover the dye with Parafilm. Its shelf life in this state is two weeks.

3) The ETS B (Electronic Transport System Buffer) should be made in advance of the assay and new buffer should be made for each day of use.

4) Create standards in marked scintillation vials using auto pipetes and ETS B to dilute bovine gamma-globulin stock solution. Bring to a total volume of 5 mls.

5) Transfer 2.5 mls of standard to clean grinding tube(use just ETS when creating reagent blank). Add one 47 mm filter and macerate with powerdrill and Teflon pestel.

6) Pour ground filter and buffer into marked scintillation vial. Rinse vessel with additional 2.5 mls

of buffer and add to vial. Thoroughly rinse tube with DIHOH water.

7) Grind all standards and samples as described above.

8) Add Ø.4 mls sample/standard to clean glass cuvette and place Ø.4 mls reagent blank in a second clean glass cuvette.

9) Quickly add 2.Ø mls of filtered dye to each cuvette and place in the spectrophotometer (reagent blank set in reference beam).

1Ø) Wait five minutes then autozero the spec at 465nm. Record the absorbance at 595nm. Calculate regression line using counts vs. concentration.

11) Readings are stable between 5 and 6Ø minutes. New reagent blanks will be necessary if analysis exceeds one hour.

Calculations:

$$\frac{\text{(ug/ml)}}{} \times \frac{\text{(mls ETS used while grinding)}}{\text{mls } H_2O \text{ filtered}} = \text{ug/ml in sample water}$$

CHAPTER III
APPENDIX B: DATA

Appendix B.1 Adenosine triphosphate (ATP) concentration (ng/l): Kintla Creek, March 1984 - March 1985

SITE		MAR	APR	MAY	JUN	JUL	SEP	NOV	JAN	MAR
I		0.561	1.110	0.669	7.420	3.800	3.890	0.930	1.930	1.180
		0.650	4.980	2.310	1.240	1.320	2.130	1.350	3.080	0.930
		0.452	5.670	0.673	5.010		2.830	3.770		1.060
	$\bar{X}$ =	0.554	3.920	1.220	4.560	2.060	2.950	2.020	2.510	1.060
II		0.778	0.440	1.670	1.300	1.130	0.880	2.380	3.050	1.010
		0.578	1.700	6.580	1.400	0.920	1.100	2.880	2.790	2.530
		0.494	1.140	9.490	2.080	0.430	1.930	1.760		2.150
	$\bar{X}$ =	0.617	1.090	3.070	1.590	0.830	1.300	2.340	2.920	1.890
III		0.453	1.440	0.935	0.960	1.900	1.711	1.920	1.120	1.370
		0.558	3.050	1.390	0.850	1.030	1.150	2.231	0.747	1.050
		0.314	0.980	1.090	0.831	0.170		1.940		1.411
	$\bar{X}$=	0.442	1.820	1.140	0.881	1.030	1.431	2.030	0.932	1.280

Appendix B.2 Particulate protein concentration (ug/l): Kintla Creek, April 1984 - March 1985

SITE		APR	MAY	JUN	JUL	AUG	SEP	NOV	JAN	MAR
I		29.0	19.5	22.1	8.3	46.0	33.6	15.0	18.0	<6.0
		30.2	18.2	36.6	11.7	35.0	32.8	15.4	15.9	<6.0
		38.9	19.7	23.2	13.1	46.0	37.5	13.8	10.2	<6.0
		37.0								
	$\bar{X}$ =	33.8	19.1	27.3	11.0	42.0	34.6	14.7	14.7	<6.0
II		23.3	12.9	21.7	11.1	46.0	20.6	11.9	15.0	<6.0
		18.7	23.8	13.4	14.4	37.0	29.8	11.7	13.3	<6.0
		25.0	21.1	18.4	5.0	29.0		11.4		<6.0
	$\bar{X}$ =	22.2	19.3	17.8	10.0	37.0	25.2	11.7	14.1	<6.0
III		6.2	6.7	6.3	7.7	30.0	17.0	10.1	<6.0	<6.0
		9.5	6.4	8.1	8.5	18.0	19.6	9.2	<6.0	<6.0
		9.8	6.1	7.3	7.7	14.0	17.9	8.6	<6.0	<6.0
		7.8								
		10.7								
	$\bar{X}$ =	8.8	6.4	7.2	7.9	20.0	18.2	9.3	<6.0	<6.0

Appendix B.3 Particulate organic carbon (POC) concentration: Kintla Creek, March 1984 - January 1985

SITE		MAR	APR	MAY	JUN	JUL	AUG	SEP	NOV	JAN
I		0.071	0.146	0.153	0.133	0.133	0.244	0.307	0.083	0.176
		0.097	0.190	0.161	0.174	0.099	0.255	0.299	0.046	0.104
		0.074	0.142	0.191		0.110	0.237	0.319	0.071	0.115
	$\bar{X}$ =	0.081	0.160	0.167	0.164	0.114	0.245	0.308	0.067	0.132
II		0.074	0.201	0.131	0.212	0.149	0.280	0.282	0.330	0.141
		0.041	0.173	0.195	0.215	0.132	0.256	0.303	0.162	0.145
		0.051	0.051	0.184	0.191	0.216	0.170	0.274	0.271	
	$\bar{X}$ =	0.056	0.186	0.173	0.214	0.150	0.270	0.285	0.246	0.143
III		0.022	0.147	0.271	0.205	0.169	0.259	0.269	0.128	0.059
		0.013	0.239	0.240	0.230	0.123	0.245	0.252	0.126	0.056
				0.232	0.231	0.131	0.241	0.254	0.058	0.055
	$\bar{X}$ =	0.017	0.193	0.248	0.222	0.141	0.248	0.258	0.104	0.057

Appendix B.4 Physical parameters: discharge (Q), alkalinity, conductivity, Kintla Creek, March 1984- March 1985

SITE	PARAMETER	MAR	APR	MAY	JUN	JUL	AUG	SEP	NOV	JAN	MAR
	Q (m^3/s)	0.48	2.62	8.14	14.21	8.88	4.09	4.34	1.40	0.57	0.27
I	ALK (mg/L)	55	47	74	60	52	57	52	65	62	58
	COND(umho/cm)	96	98	101	100	106	99	97	106	110	109
II	ALK	63	58	52	58	58	68	58	61	62	58
	COND	94	97	100	100	109	102	97	105	116	117
	Q		3.00				5.20		2.50		
III	ALK	70	72	40	62	59	46	58	60	64	60
	COND	106	105	102	103	108	101	105	111	122	122

Appendix B.5 Total hydropsychid larvae densities (total number/m²): Kintla Creek, October, December 1983

October	SITE I	SITE II	SITE III
	5908	525	469
	2280	733	236
	8539	783	333
	5350	364	92
	$\bar{X}$ = 5519 ± 2566	$\bar{X}$ = 600 ± 191	$\bar{X}$ = 280 ± 158
December			
	12203	1780	761
	3269	1225	397
	5242	2442	578
	6761	292	
	$\bar{X}$ = 6869 ± 3833	$\bar{X}$ = 1434 ± 910	$\bar{X}$ = 517 ± 104

Appendix B.6 Hydropsychid species densities (larval numbers/m²): Kintla Creek, December 1983

SITE I	1	2	3	4	$\bar{X}$ ± SD
Cheumatopsyche sp.	12089	3269	5236	6750	6836 ± 3780
Ceratopsyche cockerelli	114	0	6	11	43 ± 58
SITE II					
Cheumatopsyche sp.	697	197	527	42	366 ± 299
C. cockerelli	792	708	147	167	453 ± 344
C. oslari	197	183	158	25	141 ± 79
Hydropsyche occidentalis	94	192	164	58	127 ± 61
SITE III					
C. cockerelli	6	17			11 ± 8
C. oslari	564	264			414 ± 212
H. occidentalis	189	117			153 ± 51

CHAPTER IV
APPENDIX C: Chlorophyll Data

Appendix C.1 Chlorophyll a and phaeopigment concentration (mg/m³): Kintla Creek, November 1984, January and March 1985. SD = one standard deviation of the mean.

Station		November		January		March	
		Chl a	Pheo	Chl a	Pheo	Chl a	Pheo
I		3.572	1.337	1.224	0.081	0.132	0.031
		3.953	0.742	1.256	0.087	0.137	0.167
	$\bar{X}$	3.760	1.030	1.240	0.084	0.130	0.099
	SD	0.270	0.420	0.020	0.040	0.003	0.096
II		3.927	0.541	1.029	0.076	0.310	0.153
		2.916	0.623	1.093	0.048	0.321	0.159
	$\bar{X}$	3.170	1.061	0.310	0.062	0.310	0.160
	SD	0.360	0.057	0.040	0.020	0.008	0.004
III		1.568	0.658	0.767	0.133	0.153	0.202
		1.597	0.469	0.937	0.286	0.091	0.062
	$\bar{X}$	1.580	0.560	0.850	0.210	0.122	0.132
	SD	0.020	0.130	0.120	0.110	0.040	0.100

Appendix C.2 Regression equations and coefficients of determination (r^2) for linear regression of log transformed independent variable (distance downstream) and dependent variable (Chl a concentration). * = P <0.1, ** = P <.05, *** = P <.01, ns = not significant

Month	Regression Equation	r^2	
November '84	Y = 4.80 - 0.85X	.89	**
January '85	Y = 1.40 - 0.15X	.89	***
March	Y = 0.18 - 0.004X	.003	ns